Comparative Demography of Three Hawaiian Fruit Flies (Diptera: Tephritidae) at Alternating Temperatures

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ABSTRACT Reproductive and population parameters of melon flies, *Bactrocera cucurbitae* Coquillett, oriental fruit flies, *B. dorsalis* Hendel, and Mediterranean fruit flies, *Ceratitis capitata* (Wiedemann), were measured in environmental chambers maintained at temperatures of (maximum:minimum) 24:13, 24:24, 29:18, and 35:24 ± 1°C. Alternating temperature regimes more realistically approached the variation found in nature and produced higher parameters than an optimal constant temperature (24°C). Intra- and interspecific comparisons were done with 4 separate generations of wild fruit flies reared on a common natural host. All species attained their highest intrinsic rates of population increase at 29:18 or 35:24°C; *C. capitata* exhibited the highest intrinsic rates of increase at all temperature regimes. All species attained maximum net reproductive rates at 29:18°C, in the order *C. capitata* > *B. dorsalis* > *B. cucurbitae.* The 35:24°C regime caused reductions in net reproductive rates of all species, with *B. dorsalis* affected most strongly. Male longevity was greater than that of females for all species in all temperature regimes. Two distinctly different life history patterns were evident: (1) early reproduction, short life span, and a high intrinsic rate of increase (*C. capitata*), and (2) later onset of reproduction, longer life span, and a lower intrinsic rate of increase (*B. cucurbitae*).

KEY WORDS fruit flies, comparative demography, alternating temperature, life history patterns, r- and K-selection

GROWTH, SURVIVORSHIP, AND movement are major considerations in demographic studies of populations (Price 1997). Demographic population analysis has diverse applications: predicting life history traits, analyzing population stability and structure, estimating extinction probabilities, predicting outbreaks in pest species, and examining the dynamics of colonizing or invading species (McPeek and Kalisz 1993). Carey (1993) outlined basic approaches and presented many case histories of insect demography. To develop better pest management strategies for fruit flies, many researchers have applied demographic analysis to economically important tephritid flies (Carey 1982, Carey 1989; Vargas et al. 1984; Carey and Vargas 1985; Vargas and Nishida 1985; Vargas and Carey 1990).

Life history studies provided great impetus to development of modern evolutionary ecology (Ricklefs 1990). Life history evolution involves the balance between selection on fecundity and adult survival (Moreau 1944, Williams 1966). Different life history adaptations are favored under conditions of high and low population density relative to the carrying capacity of the environment (Cody 1966). Two contrasting strategies have become known as r- and K-selected traits, respectively, after the variables of the logistic equation for population growth (Boyce 1985, Ricklefs 1990, 1997).

Ceratitis is a tephritid fly genus of ≈65 species distributed primarily in tropical and southern Africa; *Bactrocera* includes ≈440 species distributed primarily in tropical Asia, the south Pacific, and Australia (White and Elson-Harris 1992). Both genera include broadly distributed pestiferous species (White and Elson-Harris 1992), such as Mediterranean fruit fly, *C. capitata* (Wiedemann), melon fly, *B. cucurbitae* Coquillett, oriental fruit fly, *B. dorsalis* Hendel, and the fruit fly *B. latifrons* (Hendel), which are present and economically important in the Hawaiian Islands. Hawaii is the only locality where all 4 species coexist.

The effects of temperature on development and survival of the immature stages of the 4 Hawaiian species were described recently by Vargas et al. (1996). They differed most in duration of the egg stage and least in duration of the pupal stage. Temperature also affected demographic parameters (e.g., adult survival, longevity, fecundity, and intrinsic rates of increase) of laboratory adapted strains reared at several constant temperatures (Vargas et al. 1997) on an artificial wheat diet (Tanaka et al. 1969). The optimum constant temperature for all species on the basis of fecundity was 24°C.

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The objective of the research reported here was to test all life stages of 3 economically important tephritid flies under controlled laboratory conditions that approached the variation in temperature found in nature. This article presents new information on comparative development and demography of wild strains of *C. capitata*, *B. dorsalis*, and *B. cucurbitae* reared at alternating temperatures on papaya, *Carica papaya* L., a natural host of all 3 species (Liquido et al. 1989a, b).

Materials and Methods

Wild *C. capitata*, *B. dorsalis*, and *B. cucurbitae* populations were established at the Tropical Fruit Vegetable and Ornamental Crop Research Laboratory, Honolulu, after recovery from infested fruits. These procedures were repeated 4 times. Host plants were coffee, *Coffea arabica* L., from Eleele, Kauai, HI (*C. capitata*); common guava, *Psidium guajava* L., from Waimanalo, Oahu, HI (*B. dorsalis*); and ivy gourd, *Coccinia grandis* (L.) Voigt from Waimanalo, Oahu, HI (*B. cucurbitae*). Ecological information on utilization of these host plants by these fruit flies is summarized in Vargas et al. (1983, 1995) and Uchida et al. (1990), respectively. Procedures for rearing wild fruit fly pupae from infested fruits are described in Vargas et al. (1983). The 3 species were reared simultaneously in environmental chambers (Lab-line Instruments, Melrose Park, IL) maintained at (maximum:minimum) 24:13, 24:24, 29:18, and 35:24 ± 1°C, where the 1st and 2nd temperatures refer to maximum day and minimum night temperatures, respectively. Test temperatures were assigned randomly to the various environmental chambers. Cycles consisted of 9-h periods at the minimum and maximum temperatures, and 3-h periods of increase and decrease. Relative humidity was 60 ± 10% (mean ± SD) and photoperiod was 12:12 (L:D) h.

Newly emerged adults were held in cubical cages (26.5 cm each dimension) for egg collection. Experiments were initiated by collecting eggs over a 2- to 6-h period. Samples of 100 eggs were counted under a dissecting microscope, and placed on 2-cm squares of moist blotting paper. Each square of blotting paper with eggs was placed on 250 g of fresh papaya in a screen-covered 177-ml plastic cup. Each experiment was conducted with 12 cups of papaya at each temperature regime (4 cups for each of the 3 species). Experiments were replicated 4 times with different generations of fruit flies.

Mature larvae were allowed to leave the rearing cups ad libitum to pupate in a 0.5-cm layer of moist vermiculite in 1,893-ml plastic cups. Two days before expected emergence, pupae were separated from the pupation medium and held in plastic cups until eclosion.

At eclosion, 10 pairs of newly emerged adults were placed in separate containers to assess fecundity. Adults were provided a 3:1 volumetric mixture of sugar and enzymatic yeast hydrolysate (United States Biochemical, Cleveland, OH), honey, and water. Eggs were collected by inserting a small egg-collecting receptacle into a hole on the side of the cage (Vargas et al. 1997). Egg collection chambers had small holes evenly spaced on their surfaces and contained pieces of sponge saturated with guava juice for *C. capitata* and *B. dorsalis*. Thin slices of cucumber, *Cucumis sativus* L., were placed inside collection chambers for *B. cucurbitae*. Eggs were removed from the receptacle and counted daily, spread with a small camel's-hair brush on moist blotting paper, and held in petri dishes for determination of eclosion.

The following data were collected: (1) life cycle survivorship, (2) duration of preoviposition period, and (3) fecundity and fertility. Effects of temperature regimes and species on survivorship and reproductive parameters were tested by two-way analysis of variance (ANOVA) with interaction. Tukey studentized range honestly significant difference (HSD) tests were used to identify significant main effects. When both main effects and interaction were significant, one-way ANOVA and Tukey tests were computed to assess intraspecific variation among temperatures and interspecific variation within temperatures. Morrison (1983) discussed this conservative analytical procedure. Only significant interactions are mentioned in the results. All statistical tests were conducted in SAS (SAS Institute 1987), with a $P < 0.05$ significance criterion after natural logarithmic transformations. Standard life table parameters and population age structures were calculated from daily records of mortality, fecundity, and fertility of cohorts of *C. capitata*, *B. dorsalis*, and *B. cucurbitae*. Parameter symbols, formulae and definitions are summarized in Table 1 and follow Carey (1993).

Results

Development and Survival. Developmental stage durations varied inversely with temperature regime (i.e., average daily temperature) (Table 2). Egg, larval, and pupal stages of all 3 species were markedly longer at 24:13°C than those reared at other temperature regimes. *C. capitata* had the highest median survivorship (l_x) at every immature stage in every temperature chamber, with its maximum at 24:13°C (Table 3). Median survivorship values through the adult stage are presented in Fig. 1 a–c. At the pupal stage, survivorship of both *Bactrocera* spp. was below 50% at 35:24°C. *B. cucurbitae* and *B. dorsalis* were longer lived than *C. capitata*.

Reproductive Parameters. Preoviposition periods varied significantly with temperature regime ($F = 44.32$; df = 3, 47; $P = 0.0001$) and species ($F = 30.68$; df = 2, 47; $P = 0.0001$) (Table 4). Preoviposition periods at 24:13°C were significantly longer than at 24°C. At the latter temperature, preoviposition periods were significantly longer than those at 29:18 and 35:24°C, which were not significantly different. The preoviposition period for *C. capitata* was significantly shorter than those for both *Bactrocera* spp., which were not significantly different.

Gross fecundity varied significantly with temperature regime ($F = 9.16$; df = 3, 47; $P = 0.0001$) and

Table 1. Definitions and formulae for various life table and demographic parameters (Carey 1993)

Parameter	Definition	Formula
x	Age interval in days	
l_x	Proportion of females surviving to start of the age interval	
m_x	No. of female eggs laid by average female at age x	
M_x	Total no. of eggs (males and females) laid by female at age x	
Preoviposition period	Amount of time prior to eggs being laid	
Gross fecundity rate	Theoretical natality rate during lifetime of female	$\sum_{x=\alpha}^{\beta} M_x$
Net fecundity rate	No. of eggs the average newly eclosed female will lay during her lifetime	$\sum_{x=\alpha}^{\beta} l_x M_x$
Daily reproduction	Avg no. of eggs produced per day in terms of entire female life-span	$\sum_{x=\alpha}^{\beta} M_x/(\omega - \epsilon)$
Female longevity	Life-span of female	
Male longevity	Life-span of male	
Net reproductive rate *(R_o)*	Per generation contribution of newborn females to the next generation	$\sum_{x=\alpha}^{\beta} l_x m_x$
Intrinsic rate *(r)*	Rate of natural increase in a closed population	$1 = \sum_{x=\alpha}^{\beta} e^{-rx} l_x m_x$
Mean generation time *(T)*	Time required for a newborn female to replace herself R_o-fold	$(\log_e R_o)/r$
Doubling time *(DT)*	Time required for the population to increase twofold	$(\log_e 2)/r$

species ($F = 34.03$; df = 2, 47; $P = 0.0001$). The temperature-species interaction was significant ($F = 4.78$; df = 6, 47; $P = 0.0011$). Numbers of eggs laid by *B. cucurbitae* were not significantly different at 24, 35:24, and 29:18°C; however, numbers of eggs laid at 29:18 were significantly greater than at 24:13°C. Highest numbers of eggs for all experiments were laid by *B. dorsalis* at 29:18°C. Numbers of eggs laid by *B. dorsalis* at 35:24°C were significantly lower than at the other 3 temperature regimes. Numbers of eggs laid by *C. capitata* were also highest at 29:18°C, and significantly greater than at 35:24 and 24:13°C. Each species differed significantly at 24:13°C. *B. cucurbitae* had lower fecundity than *B. dorsalis* and *C. capitata* at 24 and 29:18°C. The latter 2 species were not significantly different at these temperatures. There were no significant interspecific differences in gross fecundity at 35:24°C, which reflected significant decreases in gross fecundity of *B. dorsalis* and *C. capitata* to levels close to *B. cucurbitae.*

Net fecundity varied significantly with temperature regime ($F = 9.34$; df = 3, 47; $P = 0.0001$) and species ($F = 11.70$; df = 2, 47; $P = 0.0001$). The temperature–species interaction was significant ($F = 2.79$; df = 6, 47; $P = 0.0249$). Daily egg production varied significantly with temperature regime ($F = 27.95$; df = 3, 47; $P = 0.0001$) and species ($F = 88.77$; df = 2, 47; $P = 0.0001$). The temperature–species interaction was significant ($F = 2.86$; df = 6, 47; $P = 0.0221$).

Expected Longevity. Female longevity varied significantly with temperature regime ($F = 156.21$; df = 3, 47; $P = 0.0001$) and species ($F = 113.44$; df = 2, 47;

Table 2. Developmental times (days) (mean ± SEM) of immature stages of 3 species of fruit flies reared at 4 temperature regimes

Stage	Temp, °C (max:min.)			
	24:13	24:24	29:18	35:24
	B. cucurbitae			
Egg	2.0 ± 0.00	1.0 ± 0.00	1.0 ± 0.00	1.0 ± 0.00
Larva	9.1 ± 0.44	6.3 ± 0.13	6.2 ± 0.11	4.9 ± 0.15
Pupa	19.5 ± 0.54	11.9 ± 0.07	12.0 ± 0.13	8.8 ± 0.14
	B. dorsalis			
Egg	3.2 ± 0.20	2.0 ± 0.00	2.0 ± 0.00	2.0 ± 0.00
Larva	11.1 ± 0.34	7.7 ± 0.33	7.3 ± 0.19	7.8 ± 0.25
Pupa	24.9 ± 1.02	12.4 ± 0.25	12.2 ± 0.24	10.5 ± 0.28
	C. capitata			
Egg	4.0 ± 0.00	2.0 ± 0.00	2.0 ± 0.00	2.0 ± 0.00
Larva	10.2 ± 0.38	6.5 ± 0.12	6.7 ± 0.08	6.3 ± 0.13
Pupa	19.1 ± 0.44	11.7 ± 0.38	11.4 ± 0.29	10.6 ± 0.09

Table 3. Survivorship (median l_x) for 3 species of fruit flies reared at 4 temperature regimes

Stage	Temp, °C (max:min.)			
	24:13	24:24	29:18	35:24
	B. cucurbitae			
Egg	0.75	0.87	0.76	0.74
Larva	0.67	0.82	0.72	0.61
Pupa	0.58	0.72	0.66	0.47
	B. dorsalis			
Egg	0.74	0.85	0.83	0.75
Larva	0.72	0.83	0.78	0.65
Pupa	0.68	0.66	0.59	0.44
	C. capitata			
Egg	0.97	0.92	0.92	0.92
Larva	0.86	0.84	0.80	0.78
Pupa	0.86	0.81	0.77	0.61

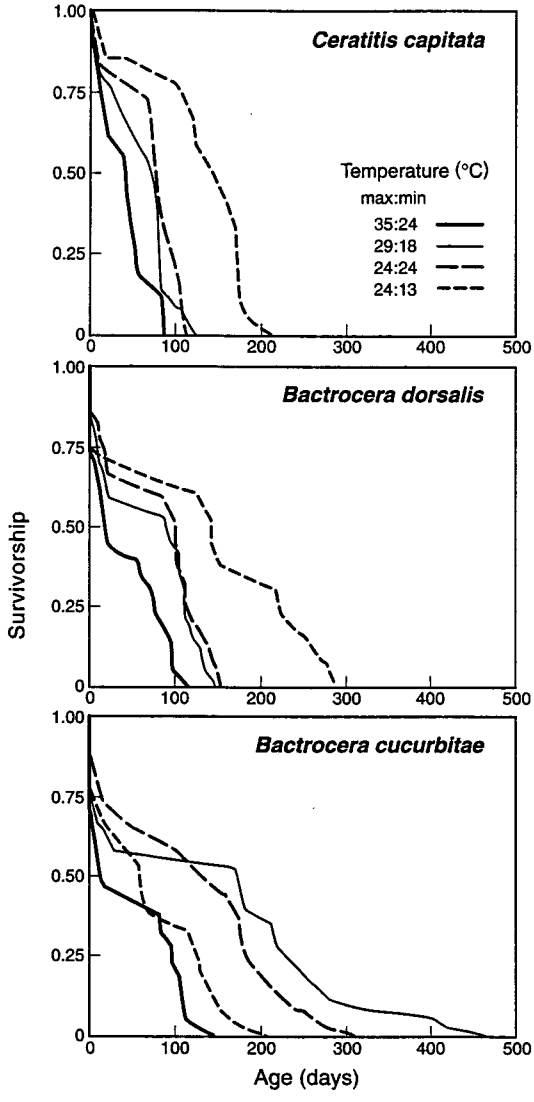

Fig. 1. Survivorship (median l_x) curves for all stages of *B. cucurbitae*, *C. capitata*, and *B. dorsalis* reared at 24:13, 24:24, 29:18, and 35:24 ± 1°C (range), where the 1st and 2nd temperatures refer to maximum day and minimum night temperatures, respectively.

$P = 0.0001$). Life span of females decreased according to the pattern 24:13 > 24 > 29:18 > 35:24°C. Female longevity differed significantly among species according to the pattern *B. cucurbitae* > *B. dorsalis* > *C. capitata.*

Male longevity varied significantly with temperature regime ($F = 205.44$; df = 3, 47; $P = 0.0001$) and species ($F = 246.12$; df = 2, 47; $P = 0.0001$). The temperature–species interaction was significant ($F = 7.73$; df = 6, 47; $P = 0.0001$). Male longevity of both *Bactrocera* spp. was significantly greater at 24:13 than at 24, 29:18 and 35:24°C; male longevity did not differ significantly between 24 and 29:18°C. Life span of males at 35:24°C was significantly less than in all other regimes. *C. capitata* exhibited greater male longevity at 24:13 than at 24, 29:18, and 35:24°C. The 29:18°C regime yielded male longevity intermediate between, but not significantly different from, 24:13 and 24°C. At 24:13°C, male longevity differed significantly according to the pattern *B. cucurbitae* > *B. dorsalis* > *C. capitata.* In the other temperature conditions, *B. cucurbitae* exhibited greater male longevity than *B. dorsalis* and *C. capitata*, which were not significantly different.

Age Structures. Several aspects of the stable age distributions of *B. cucurbitae*, *B. dorsalis*, and *C. capitata* (Table 5) were noteworthy. *B. cucurbitae* exhibited the lowest percentages of eggs and larvae in the population among the 3 species in all temperature regimes. *C. capitata*, in contrast, had the highest percentages of eggs in all temperature regimes, and the lowest percentages of pupae in all alternating temperature regimes. The percentage of adults in the *C. capitata* population at 29:18°C was less than half that of the next lowest value. Stable age distributions could not be calculated for *B. dorsalis* cohorts reared at 35:24°C.

Population Parameters. All species (Table 6) exhibited their highest intrinsic rates of increase at 29:18 or 35:24°C, with *C. capitata* highest and *B. cucurbitae* lowest. Net reproductive rates of all species exhibited increases with temperature to maxima at 29:18°C, with decreases at 35:24°C. The rate of multiplication per generation per female (R_o/100 eggs per cohort) was <1 for *B. cucurbitae* reared at all temperatures, and for *B. dorsalis* and *C. capitata* at 35:24°C. Only one cohort of *B. dorsalis* females reared at 35:24°C laid fertile eggs, therefore values obtained for all species at 35:24°C were not included in the statistical analysis. Doubling time varied significantly with temperature regime ($F = 89.93$; df = 2, 36; $P = 0.0001$) and species ($F = 46.08$; df = 2, 36; $P = 0.0001$). *C. capitata* had a significantly shorter mean doubling time than both *Bactrocera* spp. Generation time varied significantly with temperature regime ($F = 129.58$; df = 2, 36; $P = 0.0001$) and species ($F = 42.66$; df = 2, 36; $P = 0.0001$). The temperature–species interaction was also significant ($F = 3.47$; df = 4, 36; $P = 0.0207$). Mean generation times decreased with temperature in all species.

Discussion

Comparative Demography. Previous interspecific (Vargas et al. 1984, Vargas and Carey 1990) and intraspecific (Muniz and Gil 1984; Yang et al. 1994a, b) comparisons of demographic parameters for *C. capitata*, *B. dorsalis*, and *B. cucurbitae* were summarized in Vargas et al. (1997). Comparative studies of the effects of constant temperature on laboratory adapted strains reared on an artificial wheat diet indicated that adult survival, longevity, fecundity and intrinsic rates of increase varied by species and temperature (Vargas et al. 1997). The current study provides more realistic information on intra- and interspecific demographic effects of a broad range of alternating temperatures for 3 economically important fruit fly species present in

Table 4. Reproductive parameters and expectation of life of *B. cucurbitae*, *B. dorsalis*, and *C. capitata* reared at 4 temperature regimes (mean ± SEM)

Parameter	Species	Temp, °C (max.:min.)			
		24:13	24:24	29:18	35:24
Preoviposition period, days	*B. cucurbitae*	53.5 ± 6.21aA	43.2 ± 11.92bA	20.7 ± 1.23cA	15.6 ± 1.17cA
	B. dorsalis	48.4 ± 6.93aA	37.3 ± 2.66bA	18.2 ± 1.83cA	21.2 ± 3.15cA
	C. capitata	37.4 ± 5.04aB	14.9 ± 1.61bB	9.5 ± 1.15cB	8.4 ± 1.20cB
Gross fecundity, eggs/♀	*B. cucurbitae*	199.2 ± 19.32bC	236.5 ± 57.84abB	448.3 ± 80.24aB	360.9 ± 65.13abA
	B. dorsalis	952.1 ± 80.45aA	1243.9 ± 226.03aA	1296.4 ± 301.18aA	396.7 ± 112.45bA
	C. capitata	422.7 ± 41.60bB	706.2 ± 105.65abA	1036.9 ± 73.19aA	535.2 ± 99.78bA
Net fecundity, eggs/♀	*B. cucurbitae*	92.6 ± 6.36aB	108.0 ± 21.21aB	174.5 ± 28.01aB	107.5 ± 17.63aA
	B. dorsalis	371.5 ± 48.53abA	467.3 ± 122.97aA	556.6 ± 109.32aA	124.2 ± 68.55bA
	C. capitata	230.0 ± 59.35bAB	423.6 ± 99.75abA	604.0 ± 65.90aA	205.0 ± 53.03bA
Daily eggs, eggs/day	*B. cucurbitae*	0.6 ± 0.04bC	1.1 ± 0.32bB	2.8 ± 0.45aB	2.8 ± 0.37aA
	B. dorsalis	3.7 ± 0.28bA	12.4 ± 1.77aA	13.6 ± 3.48aA	8.2 ± 2.22abA
	C. ceratitis	2.7 ± 0.22bB	6.8 ± 1.28aA	11.2 ± 0.60aA	8.0 ± 1.46aA
Female longevity, days	*B. cucurbitae*	232.7 ± 10.01aA	159.0 ± 13.41bA	107.6 ± 10.58cA	87.6 ± 5.46dA
	B. dorsalis	179.8 ± 12.87aB	93.6 ± 6.02bB	83.6 ± 5.38bB	49.0 ± 2.03dB
	C. ceratitis	115.9 ± 7.58aC	75.0 ± 0.74bC	64.7 ± 1.69bC	39.7 ± 2.88dC
Male longevity, days	*B. cucurbitae*	399.8 ± 18.47aA	221.0 ± 15.48bA	180.6 ± 10.56bA	109.9 ± 3.18cA
	B. dorsalis	196.0 ± 17.59aB	107.1 ± 7.82bB	106.4 ± 5.22bB	53.1 ± 0.98cB
	C. capitata	117.9 ± 6.60aC	91.8 ± 4.41abB	110.3 ± 6.36aB	48.9 ± 2.29cB

Means in same row followed by the same lowercase letter are not significantly different (intraspecifically). Means in the same column followed by the same uppercase letter are not significantly different (interspecifically). All significant differences identified by the Tukey studentized range (HSD) test at the 0.05 level.

Hawaii. In previous demographic studies with these fruit flies, reproductive and population parameters were low or negative at the constant temperatures of 16 and 32°C (Vargas et al. 1997). In the current study, reproductive and population parameters were moderate at the alternating temperatures of 24:13 and 35:24°C. Alternating temperature regimes may provide recovery time or permit adaptation that results in higher survival and fecundity at extreme hot or cold constant temperatures.

Temperature exerted strong effects on reproductive parameters. All species exhibited reductions in survivorship and net reproductive rates at 35:24°C. *B. dorsalis* produced no fertile eggs in 4 cohorts reared at 35:24°C. This may have been the result of poor mating.

Table 5. Stable age distribution (percent; median C_x) for 3 species of fruit flies reared at 4 temperature regimes

Stage	Temp, °C (max:min.)			
	24:13	24:24	29:18	35:24
	B. cucurbitae			
Egg	12.6	14.0	19.0	23.0
Larva	22.7	29.6	34.2	32.3
Pupa	31.3	31.4	31.0	26.1
Adult	33.3	24.9	15.8	18.5
	B. dorsalis			
Egg	20.0	20.6	21.2	
Larva	35.2	35.3	35.5	
Pupa	34.3	26.6	24.7	
Adult	10.5	17.4	18.6	
	C. capitata			
Egg	23.8	28.8	35.5	30.5
Larva	35.3	33.7	39.9	35.1
Pupa	25.2	26.7	19.7	24.3
Adult	15.7	10.8	4.9	10.1

In previous studies, similar results were obtained for *B. latifrons* reared at 32°C (Vargas et al. 1997). The optimum temperature for all species, on the basis of fecundity, was apparently 29:18°C. Preoviposition periods and reproductive values at this fluctuating temperature were more favorable than at constant temperature (24°C). In previous temperature studies (Vargas et al. 1997), highest net reproductive rates (i.e., production of newborn females per generation) for all species were obtained at a constant temperature of 24°C.

In the current study, the rate of multiplication per generation per female was <1 for *B. cucurbitae* reared at all temperatures, and for *B. dorsalis* and *C. capitata* at 35:24°C. Populations held under these conditions would have a high probability of extinction. These findings suggest that extreme hot temperatures were more detrimental, and therefore possibly more limiting than cold temperatures for these species.

One major objective of this research was to improve upon previous experiments (Vargas et al. 1984, 1997; Vargas and Carey 1990) by using wild strains, a natural host, and alternating temperatures. The current study suggests that demographic parameters for climatic simulations differ when measured at constant or alternating temperatures. Nonetheless, results, whether based on constant or alternating simulations, need to be validated under field conditions. Furthermore, the physiological mechanisms responsible for increased fecundity and survival under certain temperature regimes need to be identified.

Ecological Implications. Bioclimatic studies of fruit flies have been used to predict areas where pest species may survive and reproduce (Bodenheimer 1951, Messenger and Flitters 1954). One of the most valuable applications of the "intrinsic rate of increase"

Table 6. Population parameters for *B. cucurbitae*, *B. dorsalis* and *C. capitata* reared at 4 temperature regime (mean ± SEM)

Parameter	Species	Temp, °C (max.:min.)			
		24:13	24:24	29:18	35:24
Intrinsic rate, 1/time	*B. cucurbitae*	0.034 ± 0.001	0.053 ± 0.008	0.074 ± 0.004	0.075 ± 0.006
	B. dorsalis	0.041 ± 0.002	0.065 ± 0.005	0.094 ± 0.006	0.026 ± 0.000
	C. capitata	0.051 ± 0.006	0.120 ± 0.004	0.137 ± 0.006	0.092 ± 0.008
Net reproductive rate, ♀/gen	*B. cucurbitae*	34.1 ± 2.00	42.1 ± 8.19	62.8 ± 10.25	23.0 ± 3.68
	B. dorsalis	113.9 ± 18.86	169.9 ± 41.26	197.3 ± 55.48	3.6 ± 0.00
	C. ceratitis	102.6 ± 27.33	178.0 ± 34.97	264.2 ± 31.82	22.6 ± 4.69
Doubling time, days	*B. cucurbitae*	20.7 ± 0.62aA	14.0 ± 2.15bA	9.5 ± 0.53cA	9.4 ± 0.90
	B. dorsalis	17.1 ± 1.06aB	11.0 ± 1.02bB	7.4 ± 0.45cB	26.2 ± 0.00
	C. capitata	14.0 ± 1.48aC	5.8 ± 0.16bC	5.1 ± 0.27cC	7.8 ± 0.78
Mean generation time, days	*B. cucurbitae*	105.1 ± 3.69aA	72.7 ± 7.77bA	55.8 ± 1.98cA	41.5 ± 1.99
	B. dorsalis	115.8 ± 7.53aA	78.2 ± 3.73bA	55.1 ± 2.34cA	48.2 ± 0.00
	C. capitata	88.6 ± 5.28aB	42.9 ± 0.67bB	40.7 ± 1.86cB	33.5 ± 1.46

Means in the same row followed by the same lowercase letter are not significantly different (intraspecifically). Means in the same column followed by the same uppercase letter are not significantly different (interspecifically). All significant differences identified by the Tukey studentized range (HSD) test at the 0.05 level. Only one cohort of *B. dorsalis* reared at 35:24°C laid fertile eggs, therefore data were not included in the analysis.

concept is in the delineation of the livable environment of a species (Laughlin 1965). Although all 3 tephritid species studied have tropical origins (White and Elson-Harris 1992), distribution maps reveal a broader latitudinal range for *C. capitata* than for *B. cucurbitae* or *B. dorsalis* (CAB International Institute of Entomology 1988, 1994, 1995). *C. capitata* has spread to almost all tropical and warm temperate areas of the world (White and Elson-Harris 1992). In addition, to a multivoltine habit and a broad host range of >300 different species of plants (Liquido et al. 1989b), the current study also suggests that r-selected traits allow *C. capitata* to maintain a high r-value over a broad range of temperature regimes. This tolerance may also partially explain *C. capitata*'s establishment throughout the world. Although a species of the *dorsalis* complex, the carambola fruit fly *Bactrocera carambolae* (Drew & Hancock), has been found recently outside its oriental range in Suriname in the New World (Sauers-Muller 1991), this area is tropical and near the equator.

Demographic parameters for fruit fly populations reared under different temperature regimes also have implications for examining the dynamics of colonizing or invading species. Population sizes, growth rates, and structure can be projected in relation to environmental conditions. Likewise, survival and adult longevity measured under different temperature regimes are important to understanding fruit fly invasion biology and overwintering behavior (Papadopoulos et al. 1998). These factors become important when fruit flies are introduced accidentally into new areas and eradication is considered.

Reproductive Strategies. Life history patterns are often characterized as r- or K-selected (Ricklefs 1990). Pianka (1970) hypothesized an r-K continuum with organisms positioned on it according to differences in their evolved characteristics. Common attributes of r-selected species are temperate zone distributions, small body size, early reproduction, high fecundity, short life span, and a high intrinsic rate of increase; K-selected species commonly exhibit tropical distributions, large body size, late reproduction, low fecundity, long life span, and a low intrinsic rate of increase (Pianka 1970). A necessary condition with respect to the r and K concept is that it is applied relatively (Force 1975) with respect to comparison with another organism or group of organisms. The current study makes the comparison among 3 fruit fly species. Results suggest *C. capitata* is relatively r-selected, on the basis of small body size, early onset of oviposition, high fecundity, a comparatively short life span, and a high intrinsic rate of increase. *B. cucurbitae* has a larger body size, exhibits a late onset of oviposition, much lower fecundity, greater longevity, and a lower intrinsic rate of increase; it is therefore relatively K-selected. *B. dorsalis*, with an intermediate size, exhibits mixed traits: late onset of oviposition and long life span were K-selected, whereas high fecundity and a high intrinsic rate of increase were r-selected. Previous life history and demographic studies of *B. latifrons* characterized the species as highly K-selected, with a fecundity 70% less than *B. cucurbitae* (Vargas and Nishida 1985). In conclusion, reproductive patterns may be useful characteristics for predicting the geographical range for certain groups of tephritid flies. Latitudinal gradients in fecundity patterns of birds (Ricklefs 1997) have been well documented and may also apply to the potential distribution of certain groups of insects such as tephritid flies in previously uninfested areas.

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